生 态 学 报 2010,30(15):4221—4233
Acta Ecologica Sinica

虫害诱导的植物挥发物代谢调控机制研究进展

穆　丹[1],付建玉[1],刘守安[1],韩宝瑜[1,2,*]

(1. 中国农业科学院茶叶研究所,杭州　310008;2. 中国计量学院浙江省生物计量及检验检疫技术重点实验室,杭州　310018)

摘要:长期受自然界的非生物/生物侵害,植物逐步形成了复杂的防御机制,为防御植食性昆虫的为害,植物释放虫害诱导产生的挥发性化合物(herbivore-induced plant volatiles, HIPVs)。HIPVs是植物-植食性昆虫-天敌三级营养关系之间协同进化的结果。HIPVs的化学组分因植物、植食性昆虫种类的不同而有差异。生态系统中,HIPVs可在植物与节肢动物、植物与微生物、虫害植物与邻近的健康植物、或同一植株的受害和未受害部位间起作用,介导防御性反应。HIPVs作为寄主定位信号,在吸引捕食性、寄生性天敌过程中起着重要作用。HIPVs还可以作为植物间信息交流的工具,启动植株的防御反应而增强抗虫性。不论从生态学还是经济学角度来看,HIPVs对于农林生态系中害虫综合治理策略的完善具有重要意义。前期的研究在虫害诱导植物防御的化学生态学方面奠定了良好基础,目前更多的研究转向阐述虫害诱导植物抗性的分子机制。为了深入了解HIPVs的代谢调控机制,主要从以下几个方面进行了综述。因为植食性昆虫取食造成的植物损伤是与昆虫口腔分泌物共同作用的结果,所以首先阐述口腔分泌物在防御反应中的作用。挥发物诱导素volicitin和β-葡萄糖苷酶作为口腔分泌物的组分,是产生HIPVs的激发子,通过调节伤信号诱发HIPVs的释放。接着阐述了信号转导途径对HIPVs释放的调节作用,并讨论了不同信号途径之间的交互作用。就HIPVs的代谢过程而言,其过程受信号转导途径(包括茉莉酸、水杨酸、乙烯、过氧化氢信号途径)的调控,其中茉莉酸信号途径是诱发HIPVs释放的重要途径。基于前人的研究,综述了HIPVs的主要代谢过程及其过程中关键酶类的调控作用。文中的HIPVs主要包括萜烯类化合物、绿叶挥发物和莽草酸途径产生的芳香族化合物,如水杨酸甲酯和吲哚等。作为化学信号分子,这些化合物中的一部分还能激活邻近植物防御基因的表达。萜烯合酶是各种萜烯类化合物合成的关键酶类,脂氧合酶、过氧化氢裂解酶也是绿叶挥发物代谢途径中的研究热点,而苯丙氨酸裂解酶和水杨酸羧基甲基转移酶分别是合成水杨酸及其衍生物水杨酸甲酯的关键酶类。这些酶类的基因在转录水平上调控着HIPVs代谢途径。最后展望了HIPVs的研究前景。

关键词:虫害诱导的植物挥发物;激发子;信号转导;代谢;调控机制

Advances in metabolic regulation mechanism of herbivore-induced plant volatiles

MU Dan[1], FU Jianyu[1], LIU Shouan[1], HAN Baoyu[1,2,*]

1 *Tea Research Institute of Chinese Academy of Agricultural Science*, *Hangzhou* 310008, *China*

2 *Zhejiang Provincial Key Laboratory of Biometrology and Inspection & Quarantine*, *China Jiliang University*, *Hangzhou* 310018, *China*

Abstract: During the long term of interaction between plants and the abiotic stresses, and the biotic infestation, plants have evolved complex defensive mechanisms, for instance, plants emit herbivore-induced plant volatiles (HIPVs) so as to defend themselves against herbivores. HIPVs are the results of co-evolution in tritrophic interactions among plants, herbivores and natural enemies. The chemical compositions of the volatile compounds vary with both plant and herbivorous insect species. Within the various ecosystems, HIPVs play an important role in mediating interactions between plants and arthropods, plants and microorganisms, herbivore-damaging plants and undamaged neighboring plants, as well as damaged parts and undamaged parts of the same plant, and they mediate plants defensive responses. As host location signals, HIPVs play a critical role in attracting predatory and parasitical natural enemies. HIPVs may also act as chemical communication signals among plants, and trigger defensive responses against herbivores. From an ecological or economical point of view, the

---

基金项目:国家自然科学基金资助项目(30571256);浙江省自然科学基金资助项目(Y3090531)

收稿日期:2009-11-30;　**修订日期:**2010-05-05

* 通讯作者 Corresponding author. E-mail: han-insect@263.net

research and application of HIPVs are of great importance for development of integrated pest management strategy. Previous researches significantly enriched our understanding of insect chemical ecology related to herbivore-induced plant defense. However, a great deal of attention has recently been directed towards elucidating the molecular nature of induced plant resistance. In this review, we address following key issues related to the metabolic regulation mechanisms of HIPVs. First, we discuss the functionality of oral secretions of herbivores in the defense of plants, since plant damages are resulted from both herbivore mouthpart chawing (or piercing) and oral secretions. The synomone inducers Volicitin and β-glucosidase are components of oral secretions, and trigger the release of HIPVs, at least in part, by modulating the wound signals. Subsequently, we address the signal transduction pathways and their regulatory roles in the releases of HIPVs, and discuss-the interaction among various signaling pathways. As for metabolic process of HIPVs, it is regulated by signaling pathways, including jasmonic acid (JA), salicylic acid (SA), ethylene and H_2O_2. Among which, JA has long been suggested to be an important regulator of HIPVs. Based on the previous studies, we summarize the key metabolic processes of HIPVs and the regulation roles of key enzymes in the main transduction paths. HIPVs discussed in the current paper include terpenes, green leaf volatiles and aromatic compounds derived from shikimic acid pathway such as methyl salicylate (MeSA) and indole. As chemical signaling molecules, some compounds can also activate the expression of defense genes in neighboring plants. Terpene synthases are key enzymes involved in terpenoids production. Lipoxygenase and hydroperoxide lyase are the focuses in recent researches on the metabolic pathway of green leaf volatiles. Phenylalanine ammonia lyase and salicylic acid carboxyl methyltransferase are key enzymes involved in the formation of SA and its derivative MeSA, respectively. Whereas, the genes of these enzymes regulate the metabolic pathways of HIPVs at transcription level. Finally, we give a brief outlook of the future research and application of HIPVs.

Key Words: herbivore-induced plant volatiles; elicitor; signal transduction; metabolism; regulation mechanism

在植物与植食性昆虫长期协同进化过程中,植物受植食性昆虫的为害胁迫而逐步形成了诱导性防御反应。反应早期阶段,植物体内的跨膜电势和 Ca^{2+} 浓度发生变化。这些变化通常发生在植物被害后数秒或者数分钟内,植食性昆虫口腔分泌物的特异性激发子参与调节。随后,蛋白激酶参与调控了植物与昆虫互作的反应,并与相关信号途径联系起来。信号途径被激活后,提高了一系列防御基因的表达水平,合成相关的防御化合物[1]。诱导防御反应包括直接防御和间接防御。前者是植物体通过营养限制和毒害作用直接防御害虫[2],即植物在受害后可产生对昆虫具有忌避、拒食或毒杀作用的化学物质(如具有毒性的生物碱),还可产生阻碍昆虫对食物进行消化和利用的化学物质(如蛋白酶抑制剂)[3];后者是植物释放虫害诱导产生的植物挥发性化合物(herbivore-induced plant volatiles,HIPVs),作为"求救"信号,引诱捕食性或寄生性天敌而间接防御害虫,即通常所说的植物-植食性昆虫-天敌三级营养关系中的互利素。HIPVs 引诱天敌的现象,最初是由 Turlings 等人[4]发现的。他们的研究表明,甜菜夜蛾 *Spodoptera exigua* 诱导玉米释放的萜烯类挥发物对寄生蜂 *Cotesia marginiventris* 产生明显的吸引作用。Fatouros 等[5]发现大菜粉蝶 *Pieris brassicae* 雌成虫在甘蓝上产卵亦可诱发植株释放挥发物,吸引卵寄生蜂 *Trichogramma brassicae*。另外,HIPVs 亦是植物间进行信息交流的"语言",具有系统性,可从受害部位传递至整个整株(包括地上/地下组织)、并扩散至周围健康植株,启动健康植株的防御反应而增强植物群体抗虫性[6-10]。

本文以虫害诱导植物挥发物的代谢调控机制为主线,综述了诱发 HIPVs 释放的主要诱导信号及信号转导途径,HIPVs 的主要代谢途径及途径中关键酶类物质的调控作用(以萜烯、绿叶挥发物、莽草酸途径代谢物 3 类物质为主),最后展望了 HIPVs 的研究前景。

1 诱发 HIPVs 释放的激发子及信号转导途径

1.1 HIPVs 的诱导激发子

多种生物/非生物因子都能够诱发植物产生 HIPVs。植食性昆虫为害、病原菌侵染、机械损伤等是主要

的诱导因子。但是植食性昆虫为害与机械损伤诱导产生的 HIPVs 在组分和作用效果上明显不同[11-12]。虫害不仅增加了 HIPVs 的含量和种类,而且新组分能够在损伤后较长时间内持续存在,这主要是植食性昆虫取食造成的损伤与昆虫口腔分泌物/回流物中的化学诱导物协同作用的结果[13]。用昆虫的口腔分泌物/回流物涂抹于机械损伤的植物组织上即可产生与植食性昆虫为害非常相似的 HIPVs 释放图式[14]。

大量研究表明,脂肪酸和氨基酸的共轭物(Fatty acid-amino acid conjugates, FACs),能够诱发虫害植物释放 HIPVs[15-16]。该类化合物可以从很多鳞翅目幼虫(包括天蛾科 Sphingidae、夜蛾科 Noctuidae、尺蛾科 Geometridae)的口腔回流物中分离得到,被称为挥发物诱导素。挥发物诱导素是第一个被分离纯化的对植物有诱导作用的物质[17]。例如,*N*-(17-羟基-亚麻酰基)-L-谷氨酰胺(*N*-(17-hydroxylinolenoyl)-L-glutamine),首先从甜菜夜蛾 *Spodoptera exigua* 幼虫口腔分泌物中分离得到,被命名为 volicitin[15],是一种 FAC。用 volicitin 处理玉米叶片后,植株释放的挥发物与鳞翅目幼虫直接取食后诱导产生的挥发物非常相似,均为萜烯类和吲哚的混合物[15,18]。还有 *N*-acyl Gln/Glu 等具有生物活性的 FACs,已经从部分鳞翅目幼虫的口腔分泌物中分离得到。如烟草天蛾 *Manduca sexta* 幼虫口腔分泌物中的 FAC(*N*-linolenoyl-Glu),经过研究验证,很有可能是烟草植株受虫害后释放挥发性互利素的激发子。上述 FAC 在烟草中除了能诱导挥发物的释放,亦能诱导蛋白酶抑制剂等化学防御物质的产生[19]。

Mattiacci 等[20]研究表明,β-葡萄糖苷酶(β-glucosidase)是大菜粉蝶 *Pieris brassicae* 幼虫口腔分泌物中的主要组分,该化合物很有可能是产生 HIPVs 的激发子。机械损伤的甘蓝叶片被 β-葡萄糖苷酶处理后,激发了萜烯类挥发物的释放,从而吸引菜粉蝶盘绒茧蜂 *Cotesia glomerata*。进一步研究表明,虫害甘蓝叶片与机械损伤+β-葡萄糖苷酶的叶片相比,释放的挥发物没有差别。由于 β-葡萄糖苷酶的作用,虫害甘蓝释放挥发物的量更大,持续时间更长。Hopke 等[21]研究发现,β-葡萄糖苷酶这种激发子可以诱发利马豆和玉米植株中萜烯类化合物 (*E*)-4,8-二甲基-1,3,7-壬三烯((*E*)-4,8-dimethyl-1,3,7-nonatriene, DMNT)和 (*E*,*E*)-4,8,12-三甲基-1,3,7,11-十三碳四烯((*E*,*E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene, TMTT)的合成。王霞等[22]研究表明,水稻经机械损伤加上 β-葡萄糖苷酶处理,能显著提高植株体内水杨酸 (salicylic acid, SA)、乙烯 (ethylene, ETH) 和过氧化氢的浓度。β-葡萄糖苷酶对这些信号分子含量影响的总体趋势与褐飞虱 *Nilaparvata lugens* (Stål) 为害的基本一致,表明 β-葡萄糖苷酶处理能激活与该害虫为害相类似的水稻信号转导途径。进一步研究表明,SA 信号途径参与稻飞虱 *Nilaparvata lugens* (Stål) 诱导的水稻挥发物的释放。Wang 等人[23]发现褐飞虱 *Nilaparvata lugens* 为害导致水稻中一个编码 β-葡萄糖苷酶的基因表达水平提高。在鳞翅目幼虫的唾液中还发现了其他一些水解酶,如玉米夜蛾唾液中的葡萄糖氧化酶(glucose oxidases),但是否作为激发子在植物防御反应中起作用还没有完全明确。

与上述咀嚼式昆虫相比,针对刺吸式昆虫口腔分泌物的研究还比较少。已知白粉虱 *Bemisia tabaci* 的唾液中含有碱性磷酸酶,蚜虫的唾液中含有大量水溶性消化酶,但是这些酶作为激发子在植物防御反应中的作用未得到验证[24-25]。Ma 等[26]的研究表明,麦二叉蚜 *Schizaphis graminum* 唾液中的果胶酶可能作为激发子诱发植物释放 HIPVs,从而吸引天敌防御该害虫。杜孟浩等[27]发现,褐飞虱 *Nilaparvata lugens* 口腔分泌物中含有 β-葡萄糖苷酶,使用该酶处理稻苗,稻苗释放的挥发物能够明显地吸引稻虱缨小蜂 *Anagrus nilaparvatae*。郭光喜等[28]研究证实,麦长管蚜 *Macrosiphum avenae* 的 3 龄若虫唾液中含有果胶酶成分,用果胶酶处理麦苗,诱发的挥发物对燕麦蚜茧蜂 *Aphidius avenae*、七星瓢虫 *Coccinella septempunctata* 具有明显引诱作用。最近针对蚜虫的研究表明[29],凝胶水解酶通过消化植物的细胞壁,产生蚜虫的激发子(如寡聚半乳糖醛酸)。激发子可能刺激 Ca^{2+} 离子信号通道,但尚未将下游的信号途径和挥发物的代谢途径联系起来。

植食性昆虫口腔分泌物的活性组分亦可以诱发茉莉酸(Jasmonic acid, JA)、SA 和乙烯的信号途径[30]。草地贪夜蛾 *Spodoptera frugiperda* 幼虫的口腔分泌物中含有与蛋白水解相关的成分,被称为 inceptin。Inceptin [+ICDINGVCVDA-] 和相关的肽 [+(GE)ICDINGVCVDA-] 源于叶绿体中 ATP 合成酶的 γ 亚基调控区域。这些组分能迅速激发 JA、SA 和乙烯信号途径的持续作用,从而释放萜烯类挥发物 DMNT[31-32]。烟草天

蛾 *Manduca sexta* 与宿主植物 *Nicotiana attenuata* 互作的研究表明,烟草天蛾口腔分泌物中的 FACs 能诱发 JA 和乙烯的信号途径[19, 33]。

1.2 诱发 HIPVs 的信号转导途径

近年来,有关 HIPVs 释放机理的研究表明,植物体内的信号转导途径在植食性昆虫诱导的植物挥发物释放中发挥着中心作用。调控 HIPVs 的信号传导途径非常复杂。各种诱导因子在植物体内激活不同的信号途径,进而使得与防御相关的一系列基因得到表达。植物的诱导防御反应是多种信号分子联合作用的结果,包括 SA、JA、乙烯、过氧化氢等[1]。其中 JA 信号转导途径是诱发 HIPVs 释放的关键调控因素[34]。目前在这方面的研究最多、最深入。*LOX*3 基因的过表达可以抑制 JA 的代谢途径,从而使挥发物的释放量减少[35]。利马豆中,用丙甲菌素(alamethicin, ALA)(一种有效的真菌激发子,能够诱发挥发物的释放)处理叶片,使利马豆植株体内积累 SA,从而阻碍了 JA 途径的中间体邻苯二胺(12-oxophytodienoic acid, OPDA)的合成,最终减少植株内 JA 的量,使得由 JA 信号途径调控的挥发物的合成受到阻碍[36]。另有研究表明,适当增加 OPDA,可以诱发利马豆植株内 C_{16}萜烯类物质 TMTT 的释放[37]。使用不同比例的 JA 和 SA 处理利马豆叶片,释放的挥发物(如 TMTT)强烈吸引红叶螨的捕食性天敌[38]。菜青虫 *Pieris rapae* 为害拟南芥诱发了 JA/SA 的信号途径,从而诱导了萜烯合成酶基因 *At-TPS*10,绿叶挥发物代谢途径中的关键酶基因 *AtLOX*2、*AtHPL* 等在转录水平上的高表达,促进一系列 HIPVs 的合成,并吸引微红绒茧蜂 *Cotesia rubecula* [39]。因此,JA 和 SA 两条信号途径之间既存在相互拮抗,又具有相互协调的作用,二者共同调控植物受害后的诱导防御反应,而虫害诱导植物挥发性互利素的释放则是二者谐调的结果[36]。

植食性昆虫为害导致植株体内乙烯释放量增加,在几种植物中均有报道[40-41]。同时乙烯可以增强挥发物诱导素及 JA 诱导挥发物释放的作用[40]。ETH 和 JA 作为信号途径,二者的协同作用诱发了烟草植株的防御反应,调控了相关防御基因的表达[42]。用 ETH 及其前体氨基环丙烷羧酸(1-aminocyclopropane-1-carboxylic acid, ACC)处理玉米和利马豆叶片,能显著诱发 JA 信号途径调控的挥发物的释放[41-43]。与用 JA 处理的利马豆叶片相比,用 JA 和 ETH 同时处理利马豆叶片更能吸引智利小植绥螨 *Phytoseiulus persimilis*[43]。有些研究结果表明,JA 和 ETH 两条信号途径在虫害诱导植物的防御反应中具有协同作用。

在番茄作物中,过氧化氢是植食性昆虫诱导植物防御基因表达的第二信使[44]。水稻受稻纵卷叶螟 *Cnaphalocrocis medinalis* (Guenée) 为害后,过氧化氢与 SA 含量显著提高,说明稻纵卷叶螟为害能激活水稻的过氧化氢与 SA 信号转导途径[45]。过氧化氢 / SA 信号途径能被多种咀嚼式、刺吸式昆虫口腔的分泌物激活,在植物的防御反应中起着重要作用。娄永根等[46-47]研究证实,烟草天蛾 *Nicotiana attenuate* 幼虫的为害导致烟草植株中过氧化氢与 SA 含量提高,并且过氧化氢信号途径参与烟草中防御化合物、胰蛋白酶抑制剂与二萜类糖苷(diterpene glucosides)的合成。

2 HIPVs 的代谢调控途径

目前研究较为深入的 HIPVs 主要包括萜烯类化合物、C6 绿叶挥发物以及来源于莽草酸途径的代谢物。下面以这 3 类物质为主,介绍 HIPVs 的代谢途径及途径中关键酶类物质的调控作用。

2.1 萜烯类化合物

2.1.1 萜烯类化合物的代谢途径

大多数植物遭遇虫害后均会释放萜烯类化合物。萜烯合酶(terpene synthase, TPS)等与代谢途径相关的酶的基因被激活,经过一系列酶促反应,诱导了萜类物质的合成,因此虫害诱导的萜类物质的新合成至少需要几个小时,甚至几天[48]。与健康植物相比,虫害诱导产生的萜烯类化合物的种类和相对含量均有显著提高,而且机械损伤诱发产生的萜烯类化合物的量较少[49]。因此,萜烯类化合物是虫害诱导产生的 HIPVs 的重要组分。

萜烯类化合物源于 C_5 化合物(异戊二烯单元),包括单萜(monoterpenes, C_{10})、倍半萜烯(sesquiterpenes, C_{15})、二萜(diterpenes, C_{20})等。这些萜类通过共同的前体异戊烯基二磷酸(isopentenyl diphosphate, IPP)及其

异构体二甲基烯丙基二磷酸(dimethylallyl diphosphate, DMAPP)而合成。IPP 和 DMAPP 在异戊烯基转移酶的催化作用下形成牻牛儿苗基二磷酸/香叶基二磷酸(geranyl diphosphate, GPP)、法呢基二磷酸(farnesyl diphosphate, FPP)和牻牛儿苗基牻牛儿苗基二磷酸/香叶基香叶基二磷酸(geranylgeranyl diphosphate, GGPP)。代谢途径包括以法呢基焦磷酸(farnesyl diphosphate, FPP)合成酶为关键酶的甲羟戊酸(mevalonate pathway, MVA)途径(细胞质/内质网中合成)和以牻牛儿苗基二磷酸/香叶基二磷酸(geranyl diphosphate, GPP)合成酶为关键酶的2-C-甲基赤鲜糖醇-4-磷酸(2-C-methyl-D-erythritol 4-phosphate MEP)途径(质体中合成)。MVA 和 MEP 这两条途径是相对独立的。例如,细胞质中倍半萜烯 C_{15}是由 IPP 为前体,通过 MVA 途径而合成;质体中单萜 C_{10}和双萜 C_{20}亦是由 IPP 为前体,通过 MEP 途径而合成。近年来的研究表明,这两种途径可以通过 IPP 作为交叉点,可以进行交互反应[50-51]。

2.1.2　萜烯合酶等的调控作用

TPS 是各种萜烯类化合物合成的关键酶类。TPS 种类的多样性导致萜烯类化合物结构的多样性。萜烯类化合物是以 GPP、FPP 及 GGPP 等作为底物,由一系列 TPS 催化合成。GPP 在单萜烯合酶(monoterpene synthase)作用下生成单萜,FPP 在倍半萜烯合酶(sesquiterpene synthase)作用下生成倍半萜烯,GGPP 在二萜烯合酶(diterpene synthase)作用下生成二萜。在拟南芥中,32 个基因包括 2 个赤霉素生物合成基因都是 TPS 家族成员,涉及单萜烯合酶、倍半萜烯合酶等[52]。大量研究表明,萜类化合物的合成受转录水平上 TPS 基因的调控[53-55]。调控机制非常复杂,因为虫害诱导的萜类物质的释放及 TPS 基因在转录水平上的表达受很多因素的影响(如昼夜节律性、滞后性)。利用 zNose™监测利马豆受虫害期间挥发物释放情况的研究表明,萜类的释放遵循日间节律,即与黑暗条件相比,光照条件下挥发物的释放量增大,进一步研究发现相关 TPS 基因的表达量亦明显增加[56]。云杉 *Picea sitchensis* 遭遇白松球果象 *Pissodes strobe* 为害后第 3 天开始释放单萜氧化物——芳樟醇,至第 5 天其释放量达到高峰,并且该虫害的诱导作用导致单萜合酶基因在转录水平上的表达量显著增加[57]。Schnee 等[58]在研究棉贪夜蛾-玉米-茧蜂三级营养关系时,克隆得到萜烯合酶基因 *tps*10,该基因可以调控 9 种挥发物的合成,而这些挥发物能够强烈吸引天敌。Ro 等[59]从火炬松 *Pinus taeda* 中克隆得到一个萜烯合酶基因 *PtTPS-LAS*,该酶可以催化 GGPP 形成松香二烯等。戈林泉等[60]为阐明水稻β-石竹烯在调节水稻-褐飞虱-稻虱缨小蜂相互关系中的作用,克隆鉴定了一个水稻 β-石竹烯合成酶基因 *OsCAS*。该研究结果表明,褐飞虱为害和 JA 处理均能明显上调 *OsCAS* 基因的表达水平,且该基因与同为单子叶植物玉米中的 3 个β-石竹烯合成酶基因有很高的同源性(99%)。上述结果与已知的水稻、玉米的β-石竹烯参与植物间接防御反应的结果相一致[61-63]。

除 TPS 外,萜烯类挥发物代谢途径中还有很多起重要作用的酶类。羟甲基戊二酰 CoA 还原酶(hydroxymethyl glutarylCoA reductase, HMGR),催化 HMG-CoA 形成 MVA,是 MVA 途径中一个重要的限速酶,亦是萜烯类化合物在细胞质代谢途径中的关键调控点。Jiang 等[64]从橡胶 *Eucommia ulmoides* 中克隆得到 HMGR 的一个基因 *EuHMGR*,该研究表明,在 *HMGR* 缺失的酵母突变体 JRY2394 中表达后发现,*EuHMGR* 能有效地调控 MVA 途径。另一类是异戊烯基转移酶,包括香叶基二磷酸合酶(geranyl diphosphate synthase, GPPS)、法呢基二磷酸合酶(farnesyl diphosphate synthase, FPPS)和香叶基二磷酸合酶(geranylgeranyl diphosphate synthase, GGPPS)。GPP 的研究多数集中于植物体。FPPS 广泛存在于细胞质、叶绿体、线粒体中[65-67],三齿蒿、棉花等的 FPPS 序列有 7 个保守区和 2 个特异的富含天冬氨酸的模块[68-69]。Takaya 等[70]从橡胶 *Hevea brasiliensis* 的 cDNA 文库中分离得到 1 个 *GGPPS* 基因,该基因的原核表达产物可以催化 GGPP 的生成。

值得一提的是,植物线粒体中的倍半萜合酶 sesqui-TPS(FaNES1)催化橙花叔醇(nerolidol)及 DMNT 的合成。大部分植物在遭遇虫害后都会产生这两种物质,在吸引捕食性和寄生性天敌方面起着重要作用[71]。线粒体中亦存在 FPP 合成酶及 TPS(FaNES2,为 FaNES1 的异构酶),促进了倍半萜烯的合成[72]。利马豆受虫害后释放 DMNT[73],进一步研究表明,DMNT 的释放受倍半萜合成酶的调控,该酶被虫害诱导表达,进而催化倍

半萜烯前体(3*S*)-(*E*)-neridol 的合成[74]。

2.2 绿叶挥发物

2.2.1 绿叶挥发物的代谢途径

绿叶挥发物(green leaf volatiles, GLVs)又称 C_6 挥发物,即植物挥发物中 6 个碳的醛、醇及其酯类。当植物叶片受虫害或者一些生物、非生物的胁迫时,它们由植物体内的亚油酸(linoleic acid)和 α-亚麻酸(α-linolenic acid)经脂氧合酶(lipoxygenase, LOX)、脂肪酸过氧化氢裂解酶(fatty acid hydroperoxide lyase, HPL)等一系列酶促反应而形成[75]。Assad 等[49]研究表明,虫害后不同植物体内 GLVs 的相对含量有提高亦有降低趋势,而其种类数基本上比健康植物的多,因此 GLVs 中的一些物质亦是虫害诱导性挥发物的重要组分。由于机械损伤亦能影响 GLVs 的种类及其相对含量,因此虫害诱导的 GLVs 的释放可能与植食性昆虫对植物造成的机械损伤有关。GLVs 同样可以在组织没有破损的条件下释放,即健康状态下释放 GLVs。

与萜烯类化合物的释放有所不同,植物受虫害后数秒内即可释放绿叶挥发物。拟南芥叶片组织遭受虫害后 20s 即可检测到绿叶挥发物(3*E*)-hex-3-enal[76]。该物质的释放一方面可能是因为植物体内含有大量与绿叶挥发物代谢相关的酶类,如磷脂酶(phospholipase)、LOX 和 HPL,且虫害作用导致其处于活跃状态;另一方面可能是因为这些酶与相应的底物,如 α-亚麻酸、亚油酸及 13-过氧化氢(13- hydroperoxide),在虫害作用下迅速结合[76]。

GLVs 的第一个代谢产物,顺-3-己烯醛((Z)-3-hexenal),通过 LOX 途径,由亚麻酸氧合生成 13-氢过氧化亚麻酸(linolenic acid 13-hydroperoxide, 13HPOT),后在 13-氢过氧化脂肪酸裂解酶(13-hydroperoxide lyase, 13HPL)的作用下裂解产生。正己醛(n-Hexanal)的合成途径相似,起始物源于亚油酸。反-3-己烯醛((*E*)-3-hexenal)由顺-3-己烯醛的酶/非酶异构化作用产生。这些 C_6 醛类通过醇脱氢酶(alcohol dehydrogenases)的作用可以进一步转化为 C_6 醇类,如顺-3-己烯醛转化为顺-3-己烯-1-醇((*Z*)-3-hexen-1-ol)。此后,通过脂酰基转移酶(acyltransferase)的作用,C_6 醇类转化成酯类,如顺-3-己烯-1-醇转化为顺-3-己烯-1-酯((Z)-3-hexen-1-yl acetate, Hex-Ac)[77]。

2.2.2 GLVs 与 JA / MeJA 代谢途径的联系

GLVs 和茉莉酸(Jasmonic acid, JA),还包括 JA 前体 OPDA 及其衍生物茉莉酸甲酯 MeJA 是两类不同的 oxylipins。目前,这两个 oxylipins 的代谢途径已经研究清楚,二者具有共同的前体 13HPOT。13HPOT 同时作为 13HPL(GLVs 代谢途径中的关键酶)及丙二烯氧化物合成酶(allene oxide synthase, AOS)(JA 代谢途径中的关键酶)的底物。对于 13HPOT 的利用,两条代谢途径存在竞争关系[78]。在番茄叶片中,13HPL 主要集中在质体的外包膜,以质体外部的 13HPOT 为反应物;而 AOS 主要位于质体的内包膜,以质体内部的 13HPOT 为反应物[79]。在马铃薯叶绿体中,13HPL 和 AOS 均位于类囊体膜上,但它们在膜上的功能却存在差异性[80]。oxylipins 两条不同的代谢途径是相互促进的。虫害后,两条途径同时促进虫害诱导挥发物的产生。GLVs 在虫害植物的直接防御 / 间接防御中均起着重要作用。以烟草为例,C_6 醛、醇类可以减少植株上蚜虫的数量[81]。而 JA 在防御反应的信号途径及虫害诱导的挥发性萜类化合物的合成中起着重要作用[82]。以番茄为例,体内的 C_6 醛类异构体(3*E*)-hex-2-enal 和(2*E*)-hex-3-enal 不含 β 饱和羰基基团,该活性亲电基团能诱导番茄体内萜烯类挥发物的释放、内源性 JA 的积累以及防御基因的表达[83-84]。另外,JA 能够与大分子受体结合,激活一系列目的基因的表达,生成特异性的代谢物,这与植食性昆虫诱导植物释放挥发物有关,该过程被称为类十八烷信号传递途径(Octadecanoid signaling pathway)[85]。已有研究表明,JA 诱导健康玉米、菜豆释放的挥发物,与植食性昆虫为害诱导产生的挥发物相似。水稻受外源 JA/MeJA 处理后能增加 β-石竹烯的释放量,该化合物是一类倍半萜,对稻飞虱 *Nilaparvata lugens* (Stål) 卵期寄生蜂稻虱缨小蜂 *Anagrus nilaparvatae* 具有显著的引诱效果[63, 86]。

JA 的代谢途径及其作为信号分子的重要作用已经研究得很清楚。已有的研究认为[87],JA 是长距离运输的信号物质,而寡聚半乳糖醛酸(oligogalacturonic acid, OGA)可能是局部的信号物质。有关 OGA 作为植物虫

害诱导防御信号物质的研究很多,主要集中在番茄上。目前认为,OGA 在植物防御反应中可能处于 JA 信号途径的上游或下游,通过激活 JA 途径来激活防御基因的[88]。

近年来以 13HPL 为合成关键酶的 GLVs 代谢途径的研究亦成为研究热点。Kessler 等[89]的研究显示,虫害诱导烟草释放的顺-3-己烯醇可以吸引烟草天蛾 *Manduca sexa* 的天敌;De Moraes 等[90]研究发现,虫害诱导烟草释放的 GLVs 亦对烟芽夜蛾 *Heliothis virescens* 产卵产生驱避。Bate[91]等的研究证实,反-2-己烯醛的释放能够诱导拟南芥体内 *HMGR*、*LOX* 等防御基因的表达;Arimura 等[92-93]的研究亦证明,虫害作用下莱豆叶片中顺-3-己烯醇等 GLVs 的释放,可以诱导健康莱豆体内 *LOX*、*PR*-2、*PR*-3 等防御基因的表达。上述研究表明,与 JA 途径相类似,GLVs 能够参与植物的防御反应,作为信号分子诱导相关防御基因的表达。

2.2.3　脂氧合酶等的调控作用

LOX 是 GLVs 代谢途径中的第一个酶,也是 JA 生物合成中的关键酶。LOX 基因的表达是伤口和病原物诱导的,在植物的防御反应中起着重要作用。大量研究表明,植食性昆虫的为害诱导 LOX 基因的表达量增加[94-96]。Royo 等[97]的研究表明,马铃薯中 *LOX-H*3 基因的反义缺失降低了 PIN 损伤诱导水平,从而使得植株上的害虫数量增加。虫害诱导的番茄植株中 *TomLOXD* 基因的表达在防御反应中起重要作用,该基因编码的叶绿体 LOX 是防御信号途径的组分[98]。HPL 是 GLVs 代谢途径中的关键酶,其 C_{12} 产物生成愈伤素,与植物受损的信号传递有关。例如,拟南芥的 *HPL* 基因即在损伤诱导下表达[91]。Reymond 等[99]研究表明,刺吸式昆虫的为害可以诱导 LOX 和 *HPL* 基因的表达而增大 GLVs 的释放量。Halitschke 等[35]研究证实,反-2-己烯醛代谢途径中 LOX 和 HPL 两种酶是多种植物遭受虫害后防御应答反应的重要物质。运用反义技术阻断部分 LOX 表达,减少了反-2-己烯醛等的合成和释放,降低了对害虫的抵抗,从而导致植食性昆虫数量增多。而植物 *HPL* 基因的缺失导致 GLVs 释放减少,使得蚜虫数量增加[100]。

AOS 是 JA 生物合成中的限速酶。大量研究表明,损伤可以诱导 *AOS* 基因的表达[101-102]。*AOS* 基因的表达不仅位于受害部位,而且涉及远离受害的健康组织。*AOS* 在转录水平上表达量的提高与 MeJA 含量的提高相关,由此来增强植物的防御反应能力[103]。水稻丙二烯氧化合成酶基因 *OsAOS* 是细胞色素氧化酶 CYP74A 亚家族成员,是茉莉酸合成途径中不可缺少的基因,*OsAOS* 在水稻中的超量表达能提高水稻的抗性,同时使内源茉莉酸含量和病程相关蛋白基因的表达量增大[104]。

2.3　莽草酸途径

虫害诱导的植物挥发性互利素还可以通过莽草酸(shikimate)途径合成。该途径将碳水化合物的代谢与芳香化合物的生物合成联系起来。SA、水杨酸甲酯(Methyl salicylate, MeSA)和吲哚(indole)均是由该代谢途径产生。SA 作为植物抗逆反应的信号分子,参与植物的过敏性反应(hypersensitive response, HR)和系统获得性抗病性(systemic acquired resistance, SAR),起信号传导的作用[105-106]。SA/MeSA 在植物抗病中的作用和生化、分子机理已经研究的非常清楚。近年来的研究表明,SA/MeSA 作为挥发性互利素及信号分子,在植物遭受虫害后的直接/间接防御反应中亦起着重要作用[107]。MeSA 作为植物体内重要的信号物质,能够诱导植物释放挥发性物质从而引起植物的间接防御。已有的研究表明[108],应用人工合成的虫害诱导植物挥发物或信号引导物,如外源 MeSA,在减少害虫数量和加强自然天敌种类等方面具有显著的效果。

SA/MeSA 在部分植物(拟南芥、烟草等)中的生物合成途径已经基本明确:苯丙氨酸在苯丙氨酸裂解酶(phenylalanine ammonia lyase, PAL)的作用下,首先生成反式肉桂酸(trans-cinnamic acid, CA)。PAL 是调节植物信号转导物质 SA 以及防御物质酚类化合物合成的关键酶。CA 侧链经 β 氧化和邻羟基化两种反应顺序转变生成 SA[109]。一种是 CA 侧链经 β 氧化产生苯甲酸(benzic acid, BA),后在苯甲酸羟化酶(benzoic acid 2-hydroxylase, BA_2H)作用下羟基化生成 SA;另一种是由反式肉桂酸侧链先邻羟基化产生邻香豆酸(o-coumaric acid),再经 β 氧化产生 SA[110]。SA 在水杨酸羧基甲基转移酶(salicylic acid carboxyl methyltransferase, SAMT)作用下转化成 MeSA。代谢途径中需要 3 种酶:PAL、BA_2H、SAMT,其中 PAL 和 SAMT 非常重要,其基因序列在部分植物中已经明确,各种植物之间存在不同程度的同源性。

吲哚是莽草酸途径的另一个代谢产物,由吲哚-3-磷酸甘油在吲哚-3-甘油磷酸裂解酶(indole-3-glycerol phosphate lyase, BX1)的作用下产生。甜菜粘虫能够诱导玉米幼苗产生吲哚,玉米释放的萜类和吲哚混合物可以吸引几种鳞翅目幼虫的寄生蜂[111]。而鳞翅目昆虫口腔分泌物能够激活吲哚-3-甘油磷酸化酶基因[112]。

3 HIPVs 的研究展望

综上所述,HIPVs 是植物-植食性昆虫-天敌三级营养关系研究中的热点问题。在植物-植食性昆虫-天敌的三级营养关系中,植物的上行控制作用(Bottom-up)和天敌的下行控制作用(Top-down)直接或者间接地影响着植食性昆虫的分布,是调节其种群发生和消长的重要因子[113],而 HIPVs 则是贯穿其中的“纽带”。随着化学生态学研究的深入,合理利用 HIPVs 已经成为在害虫综合治理中调控自然天敌种群数量的主要化学信息调控策略。例如,HIPVs 与植物源杀虫剂的联合使用,可以作为一项具有很大潜能的作物保护措施[114]。

HIPVs 的主要代谢途径逐渐明了,而植物与昆虫间化学通讯信号的生物诱导及相关基因调控研究还较少[115]。随着酶学和分子生物学手段的改进以及基因工程水平的不断提升,研究控制 HIPVs 生物合成的酶系统,进行基因克隆,并与分子育种和遗传改良等途径相结合,构建释放较为丰富的 HIPVs 的植株,自然地引诱环境中的天敌,而减免化学农药的施用,从而发展一种利用作物自身释放的挥发性化合物来控制害虫的新理论、新技术。

然而,迄今很多关于 HIPVs 的研究都是在实验室或者温室中完成的,今后如何有效地进行田间试验,以探究虫害植株释放 HIPVs 吸引天敌将成为昆虫化学生态学的一个重点。另外,植物地上/地下部分产生的 HIPVs 共同介导的生态抗性研究还比较少,值得深入思考,为害虫的综合防治提供新的思路[116]。

References:

[1] Arimura G, Kost C, Boland W. Herbivore-induced, indirect plant defences. Biochimica et Biophysica Acta, 2005, 1734 (2): 91-111.

[2] Chen M S, Wu J X, Zhang G H. Inducible direct plant defense against insect herbivores. Chinese Bulletin of Entomology, 2009, 46 (2): 175-186.

[3] Zeng R S, Su Y J, Ye M, Xie L J, Chen M, Song Y Y. Plant induced defense and biochemical mechanisms. Journal of South China Agricultural University, 2008, 29 (2): 1-6.

[4] Turlings T C J, Tumlinson J H, Lewis W J. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science, 1990, 250 (4985): 1251-1253.

[5] Fatouros N E, Broekgaarden C, Bukovinszkine′Kiss G, van Loon J J A, Mumm R, Huigens M E, Dicke M, Hilker M. Male-derived butterfly anti-aphrodisiac mediates induced indirect plant defense. Proceedings of the National Academy of Sciences of the United States of America, 2008, 105 (29): 10033-10038.

[6] Baldwin I T, Schultz J C. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. Science, 1983, 221 (4607): 277-279.

[7] Turlings T C J, Wäckers F. Recruitment of predators and parasitoids by herbivore-injured plants. Insect Chemical Ecology, 2004, 2: 21-75.

[8] Ton J, D′Alessandro M, Jourdie V, Jakab G, Karlen D, Held M, Mauch-Mani B, Turlings T C J. Priming by airborne signals boosts direct and indirect resistance in maize. Plant Journal, 2006, 49 (1): 16-26.

[9] Frost C J, Mescher M C, Dervinis C, Davis J M, Carlson J E, De Moraes C M. Priming defense genes and metabolites in hybrid poplar by the green leaf volatile cis-3-hexenyl acetate. New Phytologist, 2008, 180 (3): 722-734.

[10] Rasmann S, Turlings T C J. Simultaneous feeding by aboveground and belowground herbivores attenuates plant-mediated attraction of their respective natural enemies. Ecology Letters, 2007, 10 (10): 926-936.

[11] Bouwmeester H J, Verstappen F W A, Posthumus M A, Dicke M. Spider mite-induced (3*S*)-(*E*)-nerolidol synthase activity in cucumber and lima bean. The first dedicated step in acyclic C11-homoterpene biosynthesis. Plant Physiology, 1999, 121 (1): 173-180.

[12] De Moraes C M, Lewis W J, Paré P W, Alborn H T, Tumlinson J H. Herbivore-infested plants selectively attract parasitoids. Nature, 1998, 393 (6685): 570-573.

[13] Paré P W, Tumlinson J H. De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. Plant Physiology, 1997, 114 (4): 1161-1167.

[14] Halitschke R, Kessler A, Kahl J, Lorenz A, Baldwin I T. Ecophysiological comparison of direct and indirect defenses in *Nicotiana attenuata*.

Oecologia, 2000, 124 (3): 408-417.

[15] Alborn H T, Turlings T C J, Jones T H, Stenhagen G, Loughrin J H, Tumlinson J H. An elicitor of plant volatiles from beet armyworm oral secretion. Science, 1997, 276 (5314): 945-949.

[16] Spiteller D, Boland W. *N*-(17-acyloxy-acyl)-glutamines: novel surfactants from oral secretions of lepidopteran larvae. The Journal of Organic Chemistry, 2003, 68 (23): 8743-8749.

[17] Yin H D, Huang C H, Xue K, Wang R J, Yan F M. Roles of insect salivary components in insect-plant interactions. Acta Entomologica Sinica, 2006, 49 (5): 843-849.

[18] Schmelz E A, Alborn H T, Tumlinson J H. The influence of intact-plant and excised-leaf bioassay designs on volicitin- and jasmonic acid-induced sesquiterpene volatile release in *Zea mays*. Planta, 2001, 214 (2): 171-179.

[19] Halitschke R, Schittko U, Pohnert G, Boland W, Baldwin I T. Molecular interactions between the specialist herbivore *Manduca sexta* (Lepidoptera, Sphingidae) and its natural host *Nicotiana attenuata*. Ⅲ. Fatty acid-amino acid conjugates in herbivore oral secretions are necessary and sufficient for herbivore-specific plant responses. Plant Physiology, 2001, 125 (2): 711-717.

[20] Mattiacci L, Dicke M, Posthumus M A. β-glucosidase: an elicitor of herbivore-induced plant odor that attracts host-searching parasitic wasps. Proceedings of the National Academy of Sciences of the United States of America, 1995, 92 (6):2036-2040.

[21] Hopke J, Donath J, Blechert S, Boland W. Herbivore-induced volatiles: the emission of acyclic homoterpenes from leaves of Phaseolus lunatus and Zea mays can be triggered by a β-glucosidase and jasmonic acid. FEBS Letters, 1994, 352 (2): 146-150.

[22] Wang X. Influence of Infestation by Herbivores with Different Feeding Habits or Treatment by β-Glucosidase on Levels of Main Defense-Related Signals in Rice Plants. Hangzhou: Zhejiang University, 2006.

[23] Wang X L, He R F, He G C. Construction of suppression subtractive hybridization libraries and identification of brown planthopper-induced genes. Journal of Plant Physiology, 2005, 162 (11): 1254-1262.

[24] Funk C J. Alkaline phosphatase activity in whitefly salivary glands and saliva. Archives of Insect Biochemistry and Physiology, 2001, 46 (4): 165-174.

[25] Miles P W. Aphid saliva. Biological Reviews, 1999, 74 (1): 41-85.

[26] Ma R, Reese J C, Black W C, Bramel-Cox P. Detection of pectinesterase and polygalacturonase from salivary secretions of living greenbugs, *Schizaphis graminum* (Homoptera: Aphididae). Journal of Insect Physiology, 1990, 36 (7): 507-512.

[27] Du M H, Yan X C, Lou Y G, Cheng J A. Studies on active chemicals in the saliva of the rice brown planthopper (Nilaparvata lugens) that elicit the production of rice volatiles. Journal of Zhejiang University (Agriculture & Life Sciences), 2005, 31(3): 237-244.

[28] Guo G X, Liu Y, Yang J J, Ma X Z. Identification, activity and function determination of several salivary enzymes secreted by Macrosiphum avenae. Acta Entomologica Sinica, 2006, 49 (5): 768-774.

[29] Will T, van Bel A J. Induction as well as suppression: how aphid saliva may exert opposite effects on plant defense. Plant Signaling & Behavior, 2008, 3 (6): 427-430.

[30] Arimura G, Ozawa R, Nishioka T, Boland W, Koch T, Kühnemann F, Takabayashi J. Herbivore-induced volatiles induce the emission of ethylene in neighboring lima bean plants. Plant Journal, 2002, 29 (1): 87-98.

[31] Schmelz E A, Carroll M J, LeClere S, Phipps S M, Meredith J, Chourey P S, Alborn H T, Teal P E. Fragments of ATP synthase mediate plant perception of insect attack. Proceedings of the National Academy of Sciences of the United States of America, 2006, 103 (23): 8894-8899.

[32] Schmelz E A, LeClere S, Carroll M J, Alborn H T, Teal P E. Cowpea chloroplastic ATP synthase is the source of multiple plant defense elicitors during insect herbivory. Plant Physiology, 2007, 144 (2): 793-805.

[33] Winz R A, Baldwin I T. Molecular interactions between the specialist herbivore *Manduca sexta* (Lepidoptera, Sphingidae) and its natural host *Nicotiana attenuata*. Ⅳ. Insect-induced ethylene reduces jasmonate-induced nicotine accumulation by regulating putrescine *N*-methyltransferase transcripts. Plant Physiology, 2001, 125 (4): 2189-2202.

[34] Krumm T, Bandemer K, Boland W. Induction of volatile biosynthesis in the lima bean (*Phaseolus lunatus*) by leucine- and isoleucine conjugates of 1-oxo- and 1-hydroxyindan-4-carboxylic acid: evidence for amino acid conjugates of jasmonic acid as intermediates in the octadecanoid signalling pathway. FEBS Letters, 1995, 377 (3): 523-529.

[35] Halitschke R, Baldwin I T. Antisense LOX expression increases herbivore performance by decreasing defense responses and inhibiting growth-related transcriptional reorganization in *Nicotiana attenuata*. Plant Journal, 2003, 36 (6): 794-807.

[36] Engelberth J, Koch T, Schüler G, Bachmann N, Rechtenbach J, Boland W. Ion channel-forming alamethicin is a potent elicitor of volatile biosynthesis and tendril coiling. Cross talk between jasmonate and salicylate signaling in lima bean. Plant Physiology, 2001, 125 (1): 369-377.

[37] Koch T, Krumm T, Jung V, Engelberth J, Boland W. Differential induction of plant volatile biosynthesis in the lima bean by early and late intermediates of the octadecanoid-signaling pathway. Plant Physiology, 1999, 121 (1): 153-162.

[38] Shimoda T, Ozawa R, Arimura G, Takabayashi J, Nishioka T. Olfactory responses of two specialist insect predators of spider mites toward plant volatiles from lima bean leaves induced by jasmonic acid and/or methyl salicylate. Applied Entomology and Zoology, 2002, 37 (4): 535-541.

[39] Van poecke R M P, Posthumus M A, Dicke M. Herbivore-induced volatile production by *Arabidopsis thaliana* leads to attraction of the parasitoid *Cotesia rubecula*: chemical, behavioral, and gene-expression analysis. Journal of Chemical Ecology, 2001, 27 (10): 1911-1928.

[40] Schmelz E A, Alborn H T, Banchio E, Tumlinson J H. Quantitative relationships between induced jasmonic acid levels and volatile emission in *Zea mays* during *Spodoptera exigua* herbivory. Planta, 2003, 216 (4): 665-673.

[41] Schmelz E A, Alborn H T, Tumlinson J H. Synergistic interactions between volicitin, jasmonic acid and ethylene mediate insect-induced volatile emission in *Zea mays*. Physiologia Plantarum, 2003, 117 (3): 403-412.

[42] Xu Y, Chang P, Liu D, Narasimhan M L, Raghothama K G, Hasegawa P M, Bressan R A. Plant defense genes are synergistically induced by ethylene and methyl jasmonate. Plant Cell, 1994, 6 (8): 1077-1085.

[43] Horiuchi J, Arimura G, Ozawa R, Shimoda T, Takabayashi J, Nishioka T. Exogenous ACC enhances volatiles production mediated by jasmonic acid in lima bean leaves. FEBS Letters, 2001, 509 (2): 332-336.

[44] Orozco-C rdenas M L, Narváez-V squez J, Ryan C A. Hydrogen peroxide acts as a second messenger for the induction of defense genes in tomato plants in response to wounding, systemin, and methyl jasmonate. Plant Cell, 2001, 13 (1): 179-191.

[45] Wang X, Lü Y H, Wang X, Xiao Y T, Lou Y G. Influence of infestation by rice leaf folder Cnaphalocrocis medinalis on levels of defense chemicals and signal molecules in rice. Journal of Zhejiang University (Agriculture & Life Science), 2008, 34 (5): 532-539.

[46] Lou Y G, Baldwin I T. Silencing of a germin-like gene in *Nicotiana attenuata* improves performance of native herbivores. Plant Physiology, 2006, 140 (3): 1126-1136.

[47] Lou Y G, Baldwin I T. Nitrogen supply influences herbivore-induced direct and indirect defenses and transcriptional responses in *Nicotiana attenuata*. Plant Physiology, 2004, 135 (1): 496-506.

[48] Paré P W, Tumlinson J H. Plant volatiles as a defense against insect herbivores. Plant Physiology, 1999, 121 (2): 325-331.

[49] Assad M T. Inheritance of resistance to the Russian wheat aphid in an Iranian durum wheat line. Plant Breeding, 2002, 121(2): 180-181.

[50] Bick J A, Lange B M. Metabolic cross talk between cytosolic and plastidial pathways of isoprenoid biosynthesis: unidirectional transport of intermediates across the chloroplast envelope membrane. Archives of Biochemistry and Biophysics, 2003, 415 (2): 146-154.

[51] Bartram S, Jux A, Gleixner G, Boland W. Dynamic pathway allocation in early terpenoid biosynthesis of stress-induced lima bean leaves. Phytochemistry, 2006, 67 (15): 1661-1672.

[52] Aubourg S, Lecharny A, Bohlmann J. Genomic analysis of the terpenoid synthase (AtTPS) gene family of Arabidopsis thaliana. Molecular genetics and genomics, 2002, 267 (6): 730-745.

[53] McKay S A B, Hunter W L, Godard K A, Wang S X, Martin D M, Bohlmann J, Plant A L. Insect attack and wounding induce traumatic resin duct development and gene expression of (−)-pinene synthase in Sitka Spruce. Plant Physiology, 2003, 133 (1): 368-378.

[54] Dudareva N, Martin D, Kish C M, Kolosova N, Gorenstein N, Fäldt J, Miller B, Bohlmann J. (*E*)-β-ocimene and myrcene synthase genes of floral scent biosynthesis in snapdragon: function and expression of three terpene synthase genes of a new terpene synthase subfamily. Plant Cell, 2003, 15 (5): 1227-1241.

[55] Sharon-Asa L, Shalit M, Frydman A, Bar E, Holland D, Or E, Lavi U, Lewinsohn E, Eyal Y. Citrus fruit flavor and aroma biosynthesis: isolation, functional characterization, and developmental regulation of *Cstps*1, a key gene in the production of the sesquiterpene aroma compound valencene. Plant Journal, 2003, 36 (5): 664-674.

[56] Arimura G, Huber D P W, Bohlmann J. Forest tent caterpillars (*Malacosoma disstria*) induce local and systemic diurnal emissions of terpenoid volatiles in hybrid poplar (*Populus trichocarpa* × *deltoides*): cDNA cloning, functional characterization, and patterns of gene expression of (-)-germacrene D synthase, *PtdTPS*1. Plant Journal, 2004, 37 (4): 603- 616.

[57] Miller B, Madilao L L, Ralph S, Bohlmann J. Insect-induced conifer defense. White pine weevil and methyl jasmonate induce traumatic resinosis, de novo formed volatile emissions, and accumulation of terpenoid synthase and putative octadecanoid pathway transcripts in *Sitka spruce*. Plant Physiology, 2005, 137(1): 369-382.

[58] Schnee C, K llner T G, Held M, Turlings T C J, Gershenzon J, Degenhardt J. The products of a single maize sesquiterpene synthase form a volatile defense signal that attracts natural enemies of maize herbivores. Proceedings of the National Academy of Sciences of the United States of America, 2006, 103 (4): 1129-1134.

[59] Ro D K, Bohlmann J. Diterpene resin acid biosynthesis in loblolly pine (*Pinus taeda*): functional characterization of abietadiene/levopimaradiene synthase (*PtTPS-LAS*) cDNA and subcellular targeting of PtTPS-LAS and abietadienol/abietadienal oxidase (PtAO, CYP720B1). Phytochemistry, 2006, 67 (15): 1572-1578.

[60] Ge L Q, Zhou G X, Wang Q, Zhu S D, Lou Y G. Cloning and prokaryotic expression of rice gene encoding β-caryophyllene synthase and its

genetic transformation. Journal of Zhejiang University (Agriculture & Life Science), 2009,35 (4):365-371.

[61] Rasmann S, Köllner T G, Degenhardt J, Hiltpold I, Toepfer S, Kuhlmann U, Gershenzon J, Turlings T C J. Recruitment of entomopathogenic nematodes by insect-damaged maize roots. Nature, 2005, 434 (7034): 732-737.

[62] Köllner T G, Held M, Lenk C, Hiltpold I, Turlings T C J, Gershenzon J, Degenhardt J. A maize (*E*)-β-caryophyllene synthase implicated in indirect defense responses against herbivores is not expressed in most American maize varieties. Plant Cell, 2008, 20 (2): 482-494.

[63] Cheng A X, Xiang C Y, Li J X, Yang C Q, Hu W L, Wang L J, Lou Y G, Chen X Y. The rice (*E*)-β-caryophyllene synthase (OsTPS3) accounts for the major inducible volatile sesquiterpenes. Phytochemistry, 2007, 68 (12): 1632-1641.

[64] Jiang J H, Kai G Y, Cao X Y, Chen F M, He D N, Liu Q. Molecular cloning of a HMG-CoA reductase gene from *Eucommia ulmoides* Oliver. Bioscience Reports, 2006, 26 (2): 171-181.

[65] Cunillera N, Boronat A, Ferrer A. The *Arabidopsis thaliana FPS*1 gene generates a novel mRNA that encodes a mitochondrial farnesyl-diphosphate synthase isoform. The Journal of Biological Chemistry, 1997, 272 (24): 15381-15388.

[66] Sanmiya K, Ueno O, Matsuoka M, Yamamoto N. Localization of farnesyl diphosphate synthase in chloroplasts. Plant and Cell Physiology, 1999, 40 (3): 348-354.

[67] Homann V, Mende K, Arntz C, Ilardi V, Macino G, Morelli G, Bose G, Tudzynski B. The isoprenoid pathway: cloning and characterization of fungal FPPS genes. Current Genetics, 1996, 30 (3): 232-239.

[68] Koyama T, Obata S, Osabe M, Takeshita A, Yokoyama K, Uchida M, Nishino T, Ogura K. Thermostable farnesyl diphosphate synthase of Bacillus stearothermophilus: molecular cloning, sequence determination, overproduction and purification. The Journal of Biochemistry, 1993, 113 (3): 355-363.

[69] Szkopińska A, Plochocka D. Farnesyl diphosphate synthase; regulation of product specificity. Acta Biochimica Polonica, 2005, 52 (1): 45-55.

[70] Takaya A, Zhang Y W, Asawatreratanakul K, Wititsuwannakul D, Wititsuwannakul R, Takahashi S, Koyama T. Cloning, expression and characterization of a functional cDNA clone encoding geranylgeranyl diphosphate synthase of *Hevea brasiliensis*. Biochimica et Biophysica Acta, 2003, 1625 (2): 214-220.

[71] Kappers I F, Aharoni A, van Herpen T W J M, Luckerhoff L L P, Dicke M, Bouwmeester H J. Genetic engineering of terpenoid metabolism attracts bodyguards to Arabidopsis. Science, 2005, 309 (5743): 2070-2072.

[72] Aharoni A, Giri A P, Verstappen F W A, Bertea C M, Sevenier R, Sun Z K, Jongsma M A, Schwab W, Bouwmeester H J. Gain and loss of fruit flavor compounds produced by wild and cultivated strawberry species. Plant Cell, 2004, 16 (11): 3110-3131.

[73] Donath J, Boland W. Biosynthesis of acyclic homoterpenes in higher plants parallels steroid hormone metabolism. Plant Physiology, 1994, 143: 473-478.

[74] Degenhardt J, Gershenzon J. Demonstration and characterization of (*E*)-nerolidol synthase from maize: a herbivore-inducible terpene synthase participating in (3*E*)-4,8,-dimethyl-1,3,7-nonatriene biosynthesis. Planta, 2000, 210 (5): 815-822.

[75] Matsui K. Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. Current Opinion in Plant Biology, 2006, 9 (3): 274-280.

[76] Matsui K, Kurishita S, Hisamitsu A, Kajiwara T. A lipid-hydrolysing activity involved in hexenal formation. Biochemical Society Transactions, 2000, 28 (6): 857-860.

[77] D'Auria J C, Pichersky E, Schaub A, Hansel A, Gershenzon J. Characterization of a BAHD acyltransferase responsible for producing the green leaf volatile (*Z*)-3-hexen-1-yl acetate in *Arabidopsis thaliana*. Plant Journal, 2007, 49 (2): 194-207.

[78] Arimura G, Matsui K, Takabayashi J. Chemical and molecular ecology of herbivore-induced plant volatiles: proximate factors and their ultimate functions. Plant and Cell Physiology, 2009, 50(5): 911-923.

[79] Froehlich J E, Itoh A, Howe G A. Tomato allene oxide synthase and fatty acid hydroperoxide lyase, two cytochrome P450s involved in oxylipin metabolism, are targeted to different membranes of chloroplast envelope. Plant Physiology, 2001, 125 (1): 306-317.

[80] Farmaki T, Sanmartín M, Jiménez P, Paneque M, Sanz C, Vancanneyt G, León J, S nchez-Serrano J J. Differential distribution of the lipoxygenase pathway enzymes within potato chloroplasts. Journal of Experimental Botany, 2007, 58 (3): 555-568.

[81] Hildebrand D F, Brown G C, Jackson D M, Hamilton-Kemp T R. Effects of some leaf-emitted volatile compounds on aphid population increase. Journal of Chemical Ecology, 1993, 19 (9): 1875-1887.

[82] Chehab E W, Kaspi R, Savchenko T, Rowe H, Negre-Zakharov F, Kliebenstein D, Dehesh K. Distinct roles of jasmonates and aldehydes in plant-defense responses. PLoS ONE, 2008, 3 (4): 1-10.

[83] Alméras E, Stolz S, Vollenweider S, Reymond P, Mène-Saffran L, Farmer E E. Reactive electrophile species activate defense gene expression in Arabidopsis. Plant Journal, 2003, 34 (2): 205-216.

[84] Engelberth J, Alborn H T, Schmelz E A, Tumlinson J H. Airborne signals prime plants against insect herbivore attack. Proceedings of the National Academy of Sciences of the United States of America, 2004, 101 (6): 1781-1785.

[85] Lou Y G, Cheng J A. Herbivore-induced plant volatiles: primary characteristics, ecological functions and its release mechanism. Acta Ecologica Sinica, 2000, 20 (6): 1097-1106.

[86] Lou Y G, Du M H, Turlings T C J, Cheng J A, Shan W F. Exogenous application of jasmonic acid induces volatile emissions in rice and enhances parasitism of *Nilaparvata lugens* eggs by the parasitoid *Anagrus nilaparvatae*. Journal of Chemistry Ecology, 2005, 31 (9): 1985-2002.

[87] León J, Rojo E, Sánchez-Serrano J J. Wound signaling in plants. Journal of Experimental Botany, 2001, 52 (354): 1-9.

[88] Xu D, Zhang Y J, Chen Y, Guo Y Y. Mechanisms of indirect defenses in plants induced by herbivores. Plant Protection, 2009, 35 (1): 13-21.

[89] Kessler A, Baldwin I T. Defensive function of herbivore-induced plant volatile emissions in nature. Science, 2001, 291 (5511): 2141-2144.

[90] De Moraes C M, Mescher M C, Tumlinson J H. Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature, 2001, 410 (6828): 577-580.

[91] Bate N J, Rothstein S J. C_6-volatiles derived from the lipoxygenase pathway induce a subset of defense-related genes. Plant Journal, 1998, 16 (5): 561-569.

[92] Arimura G, Ozawa R, Horiuchi J, Nishioka T, Takabayashi J. Plant plant interactions mediated by volatiles emitted from plants infested by spider mites. Biochemical Systematics and Ecology, 2001, 29 (10): 1049-1061.

[93] Arimura G, Ozawa R, Shimoda T, Nishioka T, Boland W, Takabayashi J. Herbivory-induced volatiles elicit defense genes in lima bean leaves. Nature, 2000, 406 (6795): 512-515.

[94] Felton G W, Donato K K, Broadway R M, Duffey S S. Impact of oxidized plant phenolics on the nutritional quality of dietar protein to a noctuid herbivore, *Spodoptera exigua*. Journal of Insect Physiology, 1992, 38 (4): 277-285.

[95] Bell E, Mullet J E. Characterization of an Arabidopsis lipoxygenase gene responsive to methyl jasmonate and wounding. Plant Physiology, 1993, 103 (4): 1133-1137.

[96] Saravitz D M, Siedow J N. The differential expression of wound-inducible lipoxygenase genes in soybean leaves. Plant Physiology, 1996, 110 (1): 287-299.

[97] Royo J, Vancanneyt G, Pérez A G, Sanz C, Störmann K, Rosahl S, Sánchez-Serrano J J. Characterization of three potato lipoxygenases with distinct enzymatic activities and different organ-specific and wound-regulated expression patterns. The Journal of Biological Chemistry, 1996, 271 (35): 21012-21019.

[98] Heitz T, Bergey D R, Ryan C A. A gene encoding a chloroplast-targeted lipoxygenase in tomato leaves is transiently induced by wounding, systemin, and methyl jasmonate. Plant Physiology, 1997, 114 (3): 1085-1093.

[99] Reymond P, Weber H, Damond M, Farmer E E. Differential gene expression in response to mechanical wounding and insect feeding in Arabidopsis. Plant Cell, 2000 12 (5): 707-720.

[100] Vancanneyt G, Sanz C, Farmaki T, Paneque M, Ortego F, Castanera P, Sánchez-Serrano J J. Hydroperoxide lyase depletion in transgenic potato plants leads to an increase in aphid performance. Proceedings of the National Academy of Sciences of the United States of America, 2001, 98 (14): 8139-8144.

[101] Sivasankar S, Sheldrick B, Rothstein S J. Expression of allene oxide synthase determines defense gene activation in tomato. Plant Physiology, 2000, 122 (4): 1335-1342.

[102] Laudert D, Weiler E W. Allene oxide synthase: a major control point in *Arabidopsis thaliana* octadecanoid signaling. Plant Journal, 1998, 15 (5): 675-684.

[103] Harms K, Ramirez I, Pena-Cortés H. Inhibition of wound-induced accumulation of allene oxide synthase transcripts in flax leaves by aspirin and salicylic acid. Plant Physiology, 1998, 118 (3): 1057-1065.

[104] Mei C S, Qi M, Sheng G Y, Yang Y N. Inducible overexpression of a rice allene oxide synthase gene increases the endogenous jasmonic acid level, *PR* gene expression, and host resistance to fungal infection. Molecular Plant-microbe Interactions, 2006, 19 (10): 1127-1237.

[105] Seskar M, Shulaev V, Raskin I. Endogenous methyl salicylate in pathogen-inoculated tobacco plants. Plant Physiology, 1998, 116 (1): 387-392.

[106] Dempsey D A, Shah J, Klessig D F. Salicylic acid and disease resistance in plants. Critical Reviews in Plant Sciences, 1999, 18 (4): 547-575.

[107] Shulaev V, Silverman P, Raskin I. Airborne signalling by methyl salicylate in plant pathogen resistance. Nature, 1997, 385 (6618): 718-721.

[108] Cardinale B J, Harvey C T, Gross K, Ives A R. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters, 2003, 6: 857-865.

[109] Raskin I. Salicylate, a new plant hormore. Plant Physiology, 1992, 99 (3): 799-803.

[110] Deng X J, Chen X Y, Du J W. Plant Volatiles and Their Metabolic Engineering. Journal of Plant Physiology and Molecular Biology, 2004, 30 (1): 11-18.

[111] Turlings T C J, Benrey B. Effects of plant metabolites on the behavior and development of parasitic wasps. Ecoscience, 1998, 5 (3): 321-333.

[112] Frey M, Stettner C, Paré P W, Schmelz E A, Tumlinson J H, Gierl A. An herbivore elicitor activates the gene for indole emission in maize. Proceedings of the National Academy of Sciences of the United States of America, 2000, 97 (26): 14801-14806.

[113] Fu X W, Guo X R, Luo M H, Yuan G H, Hu R, Yang X Y, Li L. Effects of two tobacco species on experimental and natural population dynamics of *Helicoverpa assulta* Guenn e. Acta Ecologica Sinica, 2009, 29 (5): 2340-2348.

[114] Li Y L, Zhang Y J, Zhao K J, Lu Y H, Wu K M, Guo Y Y. Semiochemicals regulation for the host seeking behavior of parasitoid wasps in three levels of trophic relationships of plant-herbivore-natural enemy. Plant Protection, 2009, 35 (3): 7-11.

[115] Mo S S, Zhao D X, Chen Q. Advances on relationships between plant volatiles and insect behavior. Chinese Journal of Tropical Agriculture, 2006, 26 (6): 84-89.

[116] RuanW B, Zhang Y Y, Gao L, Bao X Y, Bao H H, Ci H C, Li Q S, Gao Y B. Ecological function of the defense mediated by signal substances in plant volatiles. Acta Ecologica Sinica, 2010, 30 (3): 801-807.

参考文献:

[2] 陈明顺, 仵均祥, 张国辉. 植物诱导性直接防御. 昆虫知识, 2009, 46 (2): 175(186.

[3] 曾任森, 苏贻娟, 叶茂, 谢丽君, 陈敏, 宋圆圆. 植物的诱导抗性及生化机理. 华南农业大学学报, 2008, 29 (2): 1-6.

[17] 殷海娣, 黄翠虹, 薛堃, 王戎疆, 闫凤鸣. 昆虫唾液成分在昆虫与植物关系中的作用. 昆虫学报, 2006, 49 (5): 843-849.

[22] 王霞. 不同取食习性害虫和β-葡萄糖苷酶对水稻体内重要防御相关信号分子含量的影响. 杭州: 浙江大学, 2006.

[27] 杜孟浩, 严兴成, 娄永根, 程家安. 褐飞虱唾液中诱导水稻释放挥发物的活性组分研究. 浙江大学学报(农业与生命科学版), 2005, 31 (3): 237-244.

[28] 郭光喜, 刘勇, 杨景娟, 马向真. 麦长管蚜唾液中几种酶的鉴定、活力测定与功能分析. 昆虫学报, 2006, 49 (5): 768-774.

[45] 汪霞, 吕延华, 王霞, 肖玉涛, 娄永根. 稻纵卷叶螟为害对水稻防御化合物及信号分子含量的影响. 浙江大学学报(农业与生命科学版), 2008, 34 (5): 532-539.

[60] 戈林泉, 周国鑫, 王祺, 祝树德, 娄永根. 水稻β-石竹烯合成酶基因 OsCAS 的克隆鉴定、原核表达及其遗传转化. 浙江大学学报(农业与生命科学版), 2009, 35 (4): 365-371.

[85] 娄永根, 程家安. 虫害诱导的植物挥发物:基本特征、生态学功能及释放机制. 生态学报, 2000, 20 (6): 1097-1106.

[88] 许冬, 张永军, 陈洋, 郭予元. 虫害诱导植物间接防御机制. 植物保护, 2009, 35 (1): 13-21.

[110] 邓晓军, 陈晓亚, 杜家纬. 植物挥发性物质及其代谢工程. 植物生理与分子生物学学报, 2004, 30 (1): 11-18.

[113] 付晓伟, 郭线茹, 罗梅浩, 原国辉, 胡锐, 杨新影, 李亮. 两种烟草对烟夜蛾实验种群和自然种群增长的影响. 生态学报, 2009, 29 (5): 2340-2348.

[114] 李玉利, 张永军, 赵奎军, 陆宴辉, 吴孔明, 郭予元. 寄生蜂寄主选择的化学信息调控. 植物保护, 2009, 35 (3): 7-11.

[115] 莫圣书, 赵冬香, 陈青. 植物挥发物与昆虫行为关系研究进展. 热带农业科学, 2006, 26 (6): 84-89.

[116] 阮维斌, 张园园, 高陆, 包晓颖, 包海花, 慈华聪, 李庆山, 高玉葆. 植物挥发性信号物质介导抗性的生态功能. 生态学报, 2010, 30 (3): 801-807.